OBSERVATIONS ON *PONTICOCYTHEREIS TRICRISTATA* (BRADY, 1880) FROM THE ADMIRALTY ISLANDS, PAPUA NEW GUINEA AND COMMENTS ON QUATERNARY OSTRACOD EVOLUTION WITHIN THE SW PACIFIC OCEAN

MARK THOMAS WARNE

School of Ecology and Environment, Deakin University (Melbourne Campus), 221 Burwood Highway, Burwood, Victoria 3125, Australia

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The ostracod species originally described as *Cythere tricristata* Brady, 1880 from the Admiralty Islands, Papua New Guinea, appears to belong to the SW Pacific and Australasian genus *Ponticocythereis* McKenzie, 1967 (*seusu* Warne & Whatley 1996). This interpretation is based on the presence of some posterior pointing scale-like spines on the carapace surface of this species. SEM images of the type material for *Ponticocythereis tricristata* n. comb., which are presented here for the first time, enable the clear differentiation of this species from the very similar *Ponticocythereis ichthyoderua* (Brady, 1890), *Ponticocythereis quadriserialis* (Brady, 1890) and *Ponticocythereis laingensis* (Wonters, 1981). As a consequence of the subdued manifestation of scale-like or blade-like spines on adult specimens of *P. tricristata*, this species closely resembles juvenile rather than adult specimens of some other *Ponticocythereis* species. This ontogenetic/phylogenetic relationship suggests that paedomorphic processes were significant in the Quaternary evolutionary radiation of *Ponticocythereis* species within tropical SW Pacific and Australasian regions.

Key words: Recent, Ostracoda, Papua New Guinea, Pouticocythereis tricristata, paedomorphosis, Quaternary radiation.

SPECIES of the ostraeod genus *Pouticocythereis* MeKenzie, 1967 have a SW Paeifie and Australasian biogeographical and palacobiogeographical distribution. McKenzie's (1967) original generic diagnosis was reviewed by Whatley & Titterton (1981) and Warne & Whatley (1996) to accommodate a broader range of species and to more clearly define the valve/carapace morphological criteria characteristic of *Ponticocythereis*. A detailed discussion of the differential diagnoses between *Ponticocythereis* and a number of other closely allied genera is presented in Warne & Whatley (1996).

One of the species originally collected during the 'Challenger Expedition' and described by Brady (1880) was *Cythere tricristata*. Puri & Hulings (1976) selected and designated a carapace as a lectotype for this species (BM 80.38.121) from Brady's original collections housed in the Natural History Museum, London. [While this specimen is referred to as a lectotype in Puri & Hulings (1976), it has the annotation lectoholotype on the Puri & Hulings slide mount.] This lectotype specimen was collected from off the Admiralty Islands in water depths of 29 to 46 m.

Neither Brady's (1880) original illustrations, nor Puri & Hulings' (1976) light microscope photographs of this species are of adequate quality to clearly distinguish it from a number of other subsequently described and closely related taxa, such as *Ponticocythereis laingensis* (Wouters, 1981). In addition, no seanning electron microscope images of the type material of *Ponticocythereis tricristata* n. comb. have previously been available, rendering the differential diagnosis of this species obscure and identification difficult.

Perhaps as a eonsequence of the general perception that this species belonged to the genus Actinocythereis Puri, 1953 (ie. Yassini & Jones 1987: 823), P. tricristata has typically been overlooked in studies on SW Pacific and Australasian Pouticocythereis species. For instance, no mention was made by McKenzie (1986) in his discussion of various SW Pacific Ponticocythereis species. Further, Whatley & Titterton (1981) did not compare P. tricristata to their Pouticocythereis spinosa. Similarly, Wouters (1981) did not make comparisons with *P. tricristata* when describing Actinocythereis laingensis (Wouters original generic assignment-this species herein considered to belong to Ponticocythereis). The presentation of SEM images of the lectotype of P. tricristata in this paper, enables more complete differential diagnoses for SW Pacific Ponticocythereis species.

MORPHOLOGY AND PHYLOGENY

The lectotype specimen of *P. tricristata* illustrated here is a carapace. As a consequence it has not been possible to directly view its internal valve features. However, the specimen is semi-translucent, and when viewed in transmitted light the inner lamella in the anterior of the carapace is faintly visible. This internal feature appears to possess a width typical of adult Ponticocythereis species. In addition, the specimen is assumed to be an adult because of the presence of scale-like spines on the external surface (Fig. 1C-F). This type of spine development is not generally present on juvenile specimens of Ponticocythereis species (Warne & Whatley 1996). Further, the size of this speeimen (length = 0.78 mm) is greater than or approximately equivalent to the adult size of other Pontieocythereis species occurring in tropical SW Pacific regions [ie. P. manis Whatley & Titterton, 1981 and Ponticocythereis ichthyoderma (Brady) sensu McKenzie, 1986], although all currently known tropical species are smaller than the largely temperate water Ponticocythereis militaris (Brady) sensu McKenzie, 1967 (pl. 13, fig. 4).

Lateral shape

Within the genus Ponticocythereis there are three broad groups of species which differ from each other in lateral outline. The first group includes the type species Ponticocythereis militaris Brady as well as Ponticocythereis manis Whatley & Titterton. Species within this group have very broadly rounded adult posterior lateral outlines (ie. McKenzic 1967; fig. 40). The second group of species includes Ponticocythereis iehthyoderma (Brady) seusu McKenzie, 1986 and Pouticocythereis quadriserialis (Brady) seusu McKenzie, 1986, which have slightly less broadly rounded posterior margins than the first group of species (ie. McKenzie 1986; pl. 2, figs 13-14). The third group of species includes Ponticocythereis laingensis (Wouters) and Ponticocythereis tricristata (Brady), which-relative to the other two previously outlined Ponticocythereis species groups—have acutely rounded posterior margins (ie. Wouters 1981; pl. 2, fig. 1).

Spine development

Warne & Whatley (1996) emphasised the importance of posterior pointing scale and blade-like spines as a diagnostic characteristic of *Ponticocythereis* species. *Ponticocythereis* species

can, however, also be subdivided into three species groups on the basis of the strength of this type of spine development. This subdivision in part the three shape-based subdivisions previously outlined. The first group of species possesses well developed scale or blade-like spines and includes Ponticocythereis militaris and Ponticocythereis manis. In P. militaris lateral surface spines are usually strongly blade-like, although in some specimens some spines can develop a scalc-like appearance (ie. Warne 1987: pl. 3, fig. A). In P. manis, spines are generally scalelike in well preserved adult speeimens (ie. Warne & Whatley 1996: pl. I, figs 1, 3-5, 6a, b). The second group of species includes Ponticocythereis ichthyoderma and Ponticocythereis quadriserialis, In these two species, scale-like expansions on the end of spines are less well developed than for P. manis (ic. Whatley & Titterton 1981: pl. 1, figs 1-7). Blade-like spines are not common in this second group of species suggesting a closer phylogentic link to P. manis than to P. militaris. The third group of species, which includes P. laingensis and P. tricristata, generally possess subdued terminal expansions on lateral surface spines. However, in P. tricristata, terminal spine expansions tend to be more scale-like than bladelike (Fig. 1C-F), whilst in P. laingensis spines tend to be more blade-like (ie. Wouters 1981: pl. 3, figs 2a-e).

Ontogenetic development

For *Ponticocythereis* species with well developed scale-like spines in the adult stage (ie. *P. manis*), it was noted by Warne & Whatley (1996) that scale-like spines are not developed in juvenile stages—not even in penultimate instars (ie. Whatley & Titterton 1981: pl. 2, fig. 12). As a consequence, Warne & Whatley (1996) speculated that scale-like spines might be a relatively recent evolutionary acquisition within *Ponticocythereis*. Another aspect of the ontogenetic development of most *Ponticocythereis* species, is the trend from more acutely rounded posteriors in juvenile stages to more broadly rounded posteriors in male and female adult forms (ie. Whatley & Titterton 1981: pl. 2, figs 1–5, 8–10, 12).

Phylogenetic development

One feature that distinguishes juvenile *Pontico-cythereis* spp. specimens from *Actinocythereis* spp. specimens is the posterior pointing aspect of lateral

surface spines in the former (ie. Whatley & Titterton 1981: pl. 2, fig. 12; Wouters 1981: pl. 3, fig. 2f). Further, adult specimens of the third group of *Ponticocythereis* species outlined above (ie. *P. laingensis* and *P. tricristata*), which possess

relatively poorly developed terminal spine expansions and/or acutely rounded posteriors, elosely resemble *Actinocythereis* species except for the posterior pointing aspect of lateral surface spines (Fig. 1C–E).

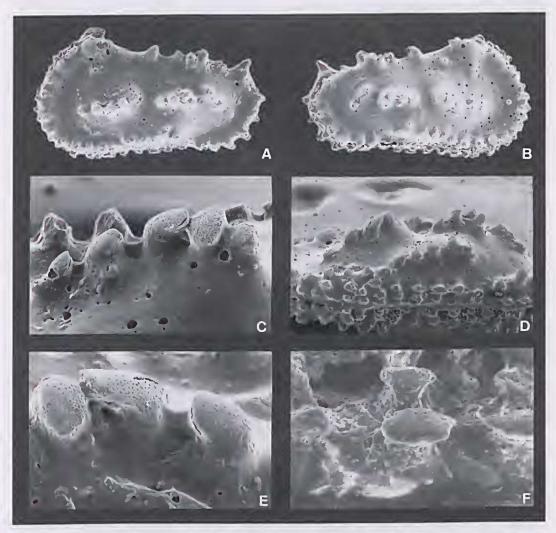


Fig. 1. Ponticocythereis tricristata (Brady, 1880); lectotype (BM 80.38.121); whole carapace; from off the Admiralty Islands, Papua New Guinea. A, external view of left valve; ×77. B, external view of right valve; ×75. C, oblique dorsal view of part of right valve showing anterior median rib spine cluster; anterior margin to left of image; ×286. D, oblique ventral view of ventral region of carapace and left valve showing ventral and median ribs and associated spine clusters; ×99. E, oblique dorsal view of part of left valve anterior median rib spine cluster; anterior margin to right of image; ×441. F, oblique ventral view of part of ventral margin of right valve showing scale-like spines; position of these spines along, ventral margin is slightly posterior of mid-length; anterior margin to left of image; ×758.

Except for the better development of a median lateral surface rib, adult specimens of *P. laingensis* and *P. tricristata* also resemble juvenile specimens of some *Ponticocythereis* species such as *P. manis*. This suggests that juvenile characteristics, with respect to spine development and posterior outline, are being held over in the adults of this third group of *Ponticocythereis* species (*P. tricristata* and *P. laingensis*). Paedomorphic processes, therefore, appear to have been significant in the evolution of this particular group of *Ponticocythereis* species.

In addition, these *Ponticocythereis* species occur within the same restricted SW Pacific/Australasian biogeographic range as other *Ponticocythereis* species which is supplementary evidence for the classification of these taxa under this genus rather than *Actinocythereis s.l.* Interestingly, current records of modern-day *Ponticocythereis* species suggest that this genus is restricted to regions east of Wallace's linc.

Evolutionary radiation

As noted by Warne (1987), the earliest currently known stratigraphical record of Ponticocythereis species is within the mid Miocene sequences of SE Australia. SE Australian fossil records suggest that Ponticocythereis species were initially adapted to warm temperate shallow marine regions with argillaceous sandy substrates. Two species arc currently recognised from temperate modern-day waters of southern Australia (McKenzie 1967; Yassini & Jones 1995). However, a greater Recent diversity of modern-day Ponticocythereis species occurs in tropical regions of the SW Pacific Ocean [ie. P. manis, P. ichthyoderma and P. quadriserialis as well as the problematic P. labiata (Brady, 1890) and P. spinosa Whatley & Titterton, 1981 (for discussion of latter see under Remarks for P. tricristata in the section on Systematic Palaeontology)].

This Quaternary diversification within *Pontico-cythereis* is part of a more general pattern of ostracod evolutionary radiation that appears to have occurred in the shallow tropical seas of the Indo-West Pacific region. For instance, *Pterobairdia* McKenzie & Keij, 1977 is perhaps the most striking example of a new taxonomic clade arising in this region during the Quaternary. If one accepts the argument presented here, that species such as *P. tricristata* and *P. laingensis* have a close phylogenetical relationship to other *Ponticocythereis* species, then paedomorphosis can be considered to be a contributing process in the adaptive radiation of Ostracoda apparent in Quaternary shallow marine realms of the SW Pacific region.

SYSTEMATIC PALAEONTOLOGY
Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA G. W. Müller, 1894
Suborder PODOCOPINA Sars, 1866
Superfamily CYTHERACEA Baird, 1850
Family TRACHYLEBERIDIDAE
Sylvester-Bradley, 1948.

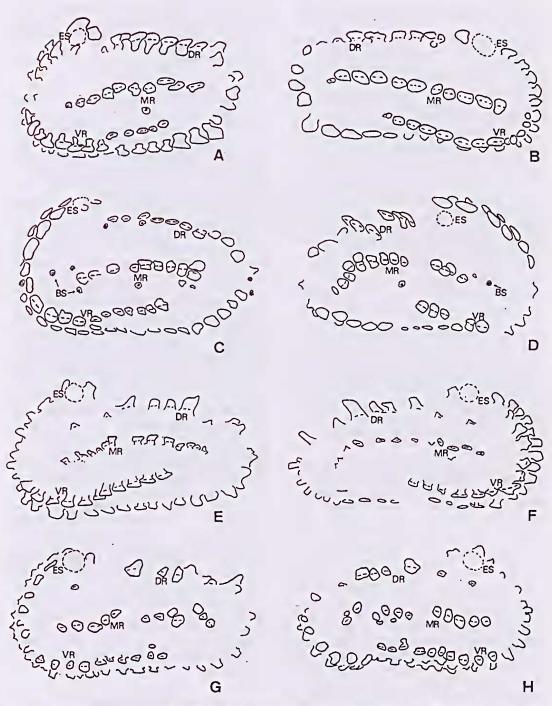
Genus Ponticocythereis McKenzie, 1967 Type species. Cythereis militaris Brady, 1866.

Ponticoeythereis tricristata (Brady, 1880) n. comb.

Figs 1A-F, 2G-H

Cythere tricristata Brady, 1880: 110–111, pl. 23, figs 6a–d.
 Cythere tricristata—Puri & Hulings, 1976: 292–293, pl. 15, figs 17–18.

Fig. 2. Spine position maps of similar SW Pacific and Australasian species of the genus Ponicocythereis McKenzie, 1976. Abbreviations: ES = eye spot; DR = dorsal rib; MR = median rib; VR = ventral rib; BS = broken spine). A, Ponticocythereis militaris (Brady, 1866) (NMV P122586); left valve; female; from latest Mioeene sands in the Sherwood 18 Borehole, Western Port Basin, Victoria, Australia (based on SEM image in Warne 1987); × 62. B, Ponticocythereis militaris (Brady, 1866) (NMV J104); right valve; male; from recent tide pool at Scaholme, Port Phillip Bay, Victoria, Australia (based on SEM image in MeKenzie 1967); × 64. C, Ponticocythereis ichthyoderma (Brady, 1890); lectotype (Hancock Museum Registration No. B453); left valve view; from recent of Sava-Sava Bay, Vanua Levu, Fiji (based on SEM image in MeKenzie 1986); × 73. D, Ponticocythereis quadriserialis (Brady, 1890); lectotype (Hancock Museum Registration No. B454); right valve view; from recent shore sand, Artillery Point, Noumea (based on SEM image in MeKenzie 1986); × 74. E, Ponticocythereis laingensis (Wouter, 1981); paratype (O.C.1091); left valve; female; from Laing Island, Hansa Bay, Papua New Guinea (based on SEM image in Wouters 1981); valve; paratype (O.C.



1092); right valve; male; from Laing Island, Hansa Bay, Papua New Guinea (based on SEM image in Wouters 1981); ×101. G, *Ponticocythereis tricristata* (Brady, 1880); left valve of lectotype (BM 80.38.121) (based on SEM image in Fig. 1); ×77. H, *Ponticocythereis tricristata* (Brady, 1880); right valve of lectotype (BM 80.38.121) (based on SEM image in Fig. 1); ×74.

Material. 1 carapace (lectotype specimen—BM 80.38. 121) housed within the Natural History Museum, London.

Additional description. SEM images of the lectotype specimen of P. tricristata (Brady) indicate that the external earapace surface has the following features. Three longitudinal ribs (dorsal, median and ventral). Dorsal rib poorly defined, possessing 9-10 mostly posteriorly oriented and pointed spines. The main clusters of dorsal rib spines occur slightly posterior of mid-length. Median rib possesses three distinct clusters of posteriorly pointing spines. In addition, the anterior-most and middle median rib clusters are of terminally bulbous (semi scale-like) spines. In dorsal view, median rib consists of two distinct humps on which the anterior-most and middle clusters of spines rest. Anterior median rib cluster consisting of 4-5 individual spines. Middle median rib cluster consisting of 4 individual spines. Posterior median rib cluster consisting of 2-3 spines. Median rib spines minutely pitted. Ventral rib consisting of approximately 10 bulbous (semi scale-like) spines with a weakly posterior pointing aspect. Spines also present along anterior, ventral and posterior valve margins, being particularly dense along ventral margin. Some ventral margin spines are strongly scale-like in appearance. The earapace surface in between the three lateral ribs is mostly smooth. Eye spot very conspicuous. Anterior margin broadly rounded; posterior margin relatively acute for the family. For other descriptive comments see Brady (1880) and Puri & Hulings (1976), although details of all internal leatures are at present incompletely known.

Remarks. The spine position maps (Fig. 2) of *P. tricristata* (Brady, 1880), *P. ichthyoderma* (Brady, 1890), *P. quadriserialis* (Brady, 1890), *P. laiugeusis* (Wouters, 1981) and *P. militaris* (Brady, 1866) indicate that different species have different adult spine cluster patterns on lateral surface ribs.

With respect to the left valve holotype specimen of P. spinosa (Whatley & Titterton 1981: pl. 1, fig. 16), there are clear differences in external earapace morphology (shape and spine development) from the lectotype carapace specimen of P. tricristata illustrated here (Fig. 1A). However, a clear distinction between the two species is not apparent when comparing the right valve paratype specimen of P. spiuosa (Whatley & Titterton 1981: pl. 1, fig. 14) with the right view of the lectotype earapace specimen of P. tricristata (Fig. 1B). Whatley & Titterton (1981) make no mention of a dual hump in the median rib in P. spiuosa, which is clearly evident in dorsal or ventral view in P. tricristata as illustrated here (Fig. 1D) as well as in Brady's 1880 original illustrations (pl. 23, figs c, d). In addition, the length of the lectotype of *P. tricristata* measured from a left valve view is 0.78 mm, which is significantly longer than the length for adult specimens of *P. spinosa* as indicated by Whatley & Titterton (1981). Further detailed consideration of the status of *P. spinosa* is beyond the scope of this paper, although it is noted that McKenzie (1986) considered *P. spinosa* to be junior synonym of *Ponticocythereis quadriserialis*. *Ponticocythereis laingensis* (Wouters, 1981) is smaller and has a less well accentuated dual hump in the median rib than *P. tricristata*. The former also tends to possess blade-like spines in the adult form whilst the later tends to possess some bulbous, semi scale-like spines.

As a further taxonomic note, a northern Australian ostracod species originally designated as Actinocythereis scutigera costata Hartmann, 1978 (pp. 87–88; text figs 156–164; pl. 5, figs 6–9), was placed in the genus Ponticocythereis by Howe & McKenzie (1989) and redesignated as the species P. costata. It possesses ornament of strong ridges and, according to Howe & McKenzie (1989), some soft part anatomical features that perhaps suggest an affinity to Ponticocythereis. Howe & McKenzie (1989) also observed that A-1 and younger juveniles of this species possess 'flat-topped spines', although they did not illustrate these features. However, these spines are perhaps similar to those found in adult specimens of some Ponticocythereis s.s. species. It is possible that the 'flat topped spines' on juvenile specimens of Pouticocythereis s.l. costata fuse to form the strong ridges present on the carapaces of adult specimens. It is here considered that this species might have a close phylogenetic relationship to Ponticocythereis s.s. 'stock'. However, the adult carapace morphology of Ponticocythereis s.l. costata falls beyond the morphological limits for Ponticocythereis as redefined by Warne & Whatley (1996), and as a consequence this species is not here considered to belong to Pouticocythereis s.s. In addition, the appearance of 'flat-topped spines' in juveniles of this species are not features that appear in juvenile specimens of Pouticocythereis s.s spp. (sensu Warne & Whatley 1996). The lectotype specimen of P. tricristata is larger (greater in length) than male and female adult specimens of Pouticocythercis s.l. costata illustrated by Hartmann (1978), preeluding the possibility that the former is a juvenile form of the later species.

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